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BY

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DISEASE RESISTANCE IN PLANTS[1]

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Individual human beings differ markedly in their susceptibility to particular diseases. In plants, which are much simpler in organisation than the higher animals, differences in reaction to disease are characteristic of the closely related varieties of which all crop plants consist. It is rare for the individual members of a variety of plant which breeds true to type to differ appreciably in susceptibility to a specific disease in the same locality.

Every cultivator of the soil, be he farmer, fruit-grower, or amateur gardener realises the value of growing varieties of crop plants true to type, for, apart from other qualities, he knows, for example, that the different varieties of potatoes, apples or roses differ enormously in their liability to disease.

With potatoes, for instance, the variety "President" is resistant to Blight while the variety "Up-to-date" is very susceptible; the variety "Great Scot" is immune from Wart disease while "King Edward" is badly attacked.

With apples, the variety "Cox's Orange Pippin" is very liable to Canker, while "Bramley's Seedling" is quite resistant to this disease.

With roses, "Dorothy Perkins" and "Crimson Rambler" are extremely susceptible to Mildew, while such a variety as "Gloire de Dijon" is practically never affected.

Certain kinds of cultivated plants are grown at periods of the year when they may completely escape attack from disease. Such varieties are not immune or even resistant to certain diseases, but they remain healthy because the germs of these diseases are not available in the air or soil to cause infection.

For example, early varieties of potatoes are only very rarely attacked by Blight because they are dug before the spores of the Blight fungus are present in the air. Such varieties are in fact quite susceptible to Blight.

[1] Lecture given at the meeting of the British Association for the Advancement of Science, Section K, Leeds, September, 1927.

In this country wheat is not often seriously affected by Black Rust, for, even when attacked, the fungus appears so late on the plants that little damage is done. Where, as in Canada, this fungus attacks wheat at an earlier stage in the growth of the plant, great damage is often done. If perchance Black Rust again threatened to seriously affect wheat in this country, attempts would be made by plant-breeders to introduce into cultivation varieties which would mature earlier than those now in use.

An important difference between plant and human diseases lies in the fact that there is extremely little evidence of anything of the nature of acquired immunity in plants. In recovery from certain human diseases, especially from some of those of parasitic origin, the individual is often rendered immune or very resistant to another attack for a considerable time. This is because the human organism in its struggle with the diseased condition has elaborated anti-bodies, which persist and afford a measure of protection after recovery has taken place. With plants, recovery from disease generally confers no degree of resistance against a renewed attack. A plum tree which has recovered from Silver-leaf disease may be quite readily infected with this disease again immediately after recovery has taken place.

It is a matter of common knowledge that many plants, grown at a time when the germs of disease are present in abundance, remain more or less immune from attack. It is clear therefore that such plants must have some means of protection.

It is of course conceivable that structural differences between resistant and susceptible varieties account for the prevention of attack in the former class. This is in fact partly true.

A somewhat thicker cuticle over the leaf may prevent invasion by those fungi the germ tubes of which effect entry into the tissues by penetration of the cuticle. One often sees that young leaves are attacked by a certain fungus, whereas mature leaves of the same plant are not so attacked. Thus *Puccinia graminis* can only infect young barberry leaves. The reason for non-infection of mature leaves is that their cuticle is so thick that the germ tubes cannot penetrate it.

Botrytis spores often infect slightly cuticularised parts such as flowers, whereas they cannot usually infect healthy, fully cuticularised organs such as mature leaves unless additional saprophytic nourishment is provided.

One of the worst diseases of apples and pears is "Scab." This

affects the twigs and leaves, and causes the unsightly, black blotches so often seen on the fruit. In susceptible varieties the germ tubes of the fungus penetrate the cuticle of the young leaf or fruit, and a mycelium is quickly established below the cuticle, which grows laterally and gives rise to conidiophores that push off the outer skin and appear as a blackish covering. Certain varieties of apple and pears are very resistant to this disease, at any rate in most seasons. In these almost immune varieties the young leaves and fruits are penetrated by the germ tubes of the spores and the fungus begins to grow laterally in the cuticle (14). Development, however, is feeble, and the fungus dies without producing conidiophores, so that to the naked eye no scab is apparent on the fruit. Here it seems that in the resistant varieties the fungus is gradually starved out, or, alternatively, that some toxic substance is secreted by the host.

The amount of sclerenchyma in the tissues may be the factor determining whether the host plant is only slightly affected or severely attacked. In the United States the variety of wheat "Webster" is highly resistant to attack by many forms of *P. graminis*, and this has been shown to be correlated with a particularly profuse development of sclerenchyma in the stem (10). The abundant sclerenchyma greatly checks the progress of the rust mycelium in the tissues.

Potato varieties show considerable differences in the susceptibility of their tubers to potato Blight. *Phytophthora infestans* infects potato tubers through the lenticels or through the eyes. As regards attack through the lenticels it has been shown that tubers which remain free from blight often have lenticels which are markedly suberised (7). Owing to the impregnation of the walls of the lenticel cells with corky substances the delicate hyphae of the fungus cannot pass through them, and invasion is barred.

Apart from the differences between young and old plant organs, all the structural features just referred to can be looked upon as being the result of essential protoplasmic differences between variety and variety. In the great majority of cases no obvious structural differences between susceptible and resistant varieties can be detected, and resistance is dependent upon protoplasmic differences too subtle to be analysed by present methods. In disease-resistant varieties of this class the parasite successfully effects entry into the tissues, but, accompanying or following this, the host reacts in some way so as to prevent the parasite from proceeding further. Thus although the initiation of infection is safely accomplished, the parasite cannot proceed further on account of the reaction of the

host. A struggle is fought out between host and parasite, and in these resistant varieties of plants the parasite is defeated.

In recent years much work has been done in trying to elucidate the nature of the struggle between host and parasite in these resistant varieties. In some cases the story of this struggle is of a surprising character.

One of the first investigations of this kind was that concerning the resistance of certain varieties of wheat to Yellow Rust. Varieties of wheat resistant to this rust such as "Einkorn" and "American Club" often show innumerable yellow flecks in the leaves, which are now known to be areas where the fungus has unsuccessfully tried to establish itself. In the variety "Einkorn," which is practically immune, the spores germinate on the leaves, and their germ tubes pass successfully through the stomata. Having safely negotiated the stomata the advancing hyphae come into contact with the cells below the stomata: the attack by these hyphae is so violent or the host cells are so weak that the latter are immediately killed (8). In this way a barrier of dead cells is erected around the fungus which the latter cannot pass, for rust fungi can only continue to live when in contact with living cells of their hosts. This is an astonishing result, and it appears that immunity from attack in such a case is due to too violent an onslaught on the part of the fungus, which prevents the establishment of the common life between host and parasite necessary for the continued existence of the latter. With the variety "American Club," which is not quite so highly resistant as "Einkorn," there is a more extended struggle: occasionally the fungus establishes itself in the tissues by sending haustoria into the still living cells, with the result that the mycelium may grow sufficiently to be able to form a few spores. In varieties fully susceptible to Yellow Rust the fungus and host cells live a common life together, and although food material is withdrawn by the fungus the host cells maintain their life.

With other wheat rusts also similar phenomena have been described: many varieties of wheat resistant to Black Rust in the United States have been shown to owe their resistance to a too vigorous initial onslaught on the part of the parasite, leading to the death of the host cells in the immediate vicinity. Workers in the United States speak of such varieties as being hyper-sensitive to the parasite.

With the variety of wheat "Mindum," which is immune in the United States to a certain form of Black Rust, the fungus actually

establishes haustoria in the cells below the stomata; these cells, however, react violently to the presence of the fungus, with the result that both the haustoria and the cells are killed (1). The infecting hyphae establish other haustoria, but as the cells again react in the same way, the infecting hyphae become exhausted and the host remains immune.

On the other hand, the resistance of some wheat varieties to these rusts may be found not to be due to initial excessive violence, but to too weak an attack, leading to failure to establish haustoria in the host cells. In this way the parasite may be starved out.

In this connection it is interesting to note that when the spores of rust fungi are put upon the wrong hosts the germ tubes successfully pass through the stomata and the preliminaries to successful infection are accomplished; but with failure to establish intimate contact with the host cells the young hyphae quickly perish (5).

In other diseases the nature of the reaction of the host in resistant varieties is entirely different. The variety of plum "Victoria" is very susceptible to Silver-leaf disease, whereas the variety "Pershore" is markedly resistant. When *Stereum purpureum*, the cause of Silver-leaf disease, attempts to infect a fresh exposure of the woody tissues of a Pershore plum the sequence of events is as follows. Many of the spores on coming into contact with the exposed surface under moist conditions are sucked into the vessels, where they germinate without danger of desiccation. A mycelium is quickly formed and this grows downwards through the wood. As with successful infection of a Victoria plum tree the progress of the fungus is accompanied by the formation of large quantities of gum from the food substances in the wood, the accumulation of which causes a marked discoloration of the wood. With the Pershore variety, however, as time goes on, so much gum is formed by the reaction of the host to the parasite that around the periphery of the invaded tissues a barrier of gum is established, which is so dense that the fungus cannot penetrate it (3). The parasite cannot proceed further and is occluded. Sooner or later it dies, and successful infection is prevented. Here also, although the initiation of infection is accomplished by the fungus, full infection does not result owing to the host's reaction.

Fresh wounds in the Victoria plum are very susceptible to infection by *Stereum purpureum* throughout the year except during the months of June, July and August. During the summer this usually susceptible variety is extremely resistant to invasion. Owing

to the tree being in a different physiological state in the summer it is able to form more profuse quantities of gum than at other times of the year. If spores of the fungus alight on a fresh wound in the wood during the summer, the initiation of infection is begun, but so much gum is produced that the progress of the fungus is quickly stopped. A gum barrier has again been formed which prevents the fungus from proceeding further. It is of interest that the phenomena associated with the inability to infect a susceptible variety during a certain period of the year are of the same kind as those associated with the prevention of invasion in a resistant variety.

It is now well known that trees affected by Silver-leaf disease sometimes regain their health. In these cases also a gum barrier has been formed by the host around the invaded tissues, which prevents the fungus from proceeding further. The result is that the fungus is confined to the zone already invaded, and it is only a question of time before it dies out.

It has been shown that with parasites which invade the woody parts of plants the excessive formation of gummy substances often prevents extensive invasion. With organisms which chiefly invade parenchymatous tissues, particularly in stems and stem-like organs, the commonest type of reaction is the formation of a cork barrier just beyond the region reached by the parasite. In general, corky cells cannot be permeated by fungal hyphae, so that these cork barriers often effectively bar the way. Familiar instances of the formation of these cork barriers are afforded in the diseases known as Larch Canker and Apple Canker. The fungus of larch canker or the fungus of apple canker progresses actively in the bark during the winter, but in the spring or summer the host temporarily checks the invader by the formation of a cork barrier. In the autumn the fungus often evades the barrier and the canker is extended. Sometimes, however, the cork barriers successfully keep the fungus at bay, especially in larch trees which are growing vigorously.

With some varieties of cultivated plants the quality of resistance to certain fungus diseases is bound up with the capacity of the variety to readily form these cork barriers in response to attempted invasion.

One of the serious diseases of cultivated flax is a wilt caused by the invasion of the root system by a species of *Fusarium* from the soil. In susceptible varieties the mycelium passes from the surface of the root to the vascular tracts, but, in resistant varieties, as soon as penetration of the root cortex has begun, a corky barrier is laid

down in the immediate vicinity, which prevents the fungus from entering the vessels (11). The consequence is that varieties able to react in this way remain unaffected by the wilt disease.

As will be explained later, the resistance of certain varieties of plants to specific diseases can nearly always be broken down by exposing the plants to unfavourable environmental conditions. Salmon (9) was able to break down the resistance of barley to the wheat form of mildew by wounding the barley leaves. With Wart disease of potatoes, however, a variety of potato immune from the disease remains immune under all known conditions. Miss Glynne (6) has recently shown that a few varieties, previously thought to be immune as the result of field observations, form very small warts when inoculated with the fungus under laboratory conditions; such varieties are therefore slightly susceptible. In susceptible types the invasion of superficial cells of the eyes of the tuber is followed by extreme proliferation and division of the neighbouring cells, with the result that a large warty excrescence is formed. With the immune types the parasite also effects entry into the surface cells of the eyes; in those varieties described by Miss Glynne as producing small warts in the laboratory there is some proliferation and abnormal division of the neighbouring host cells. In truly immune varieties the presence of the fungus causes no obvious response on the part of the host, and the fungus dies in the host cell it has penetrated. The result is that no wart is formed, and from the practical standpoint the variety is "immune." It is clear that in cases of this kind immunity is bound up with a particular protoplasmic quality of the host, which prevents the response that accompanies successful invasion of a susceptible variety.

One of the most interesting examples of disease resistance is that exhibited by coloured varieties of onions to the disease known as "smudge," which is prevalent in North America. White varieties of onions are badly affected by this disease, which causes the development of black blotches on the bulbs. Onions with a coloured skin are almost completely immune from this disease, and it has been shown that this immunity is dependent upon the anthocyanin pigments or to bodies closely associated with them (12). A solution of these pigments prevents germination or causes abnormal germination of the spores, and is also highly toxic to the mycelium of the fungus. If the red skin of an onion is wounded, so that cells devoid of pigment become exposed to the fungus, the disease is established as readily as in white varieties. It is suggested that in nature small

quantities of the pigments diffuse out from the dead outer cells of the coloured varieties and inactivate the fungus in the adherent soil.

In discussing Wart Disease of potatoes it was indicated that, generally speaking, the resistance of varieties of cultivated plants to specific diseases was modifiable within certain limits according to environmental conditions. In dealing with any kind of parasitic attack we have to take into consideration both the inherent constitution of the host with regard to resistance and the particular environmental conditions under which the plant is grown. The latter may be unfavourable to the host, preventing it from reacting to the parasite in the usual manner, thereby allowing disease to become established, or, alternatively, the environment may particularly favour the fungus in some way. The result in either case is the establishment of disease in what is usually a resistant variety. Sometimes the degradation of the variety is so marked that its inherent resistant character is almost completely masked.

Thus, if varieties of wheat normally resistant to Yellow Rust are grown in soil which is manured excessively with nitrogen, it is practically certain that they will become moderately affected. "Einkorn" wheat, which is almost immune to Black Rust as well as to Yellow Rust under ordinary conditions, may be severely affected by Black Rust in the Ganges Valley during the very hot weather of May. In both instances the inherent resistance has been profoundly modified, in one case by the chemical nature of the soil and in the other by temperature. We do not yet know precisely in what way this marked alteration in response of the host to parasitic attack is brought about.

In general there are two chief groups of factors in the environment which are capable of modifying the inherent resistance of a plant. These are soil and weather. The conditions of soil and weather are partly interdependent, for both rainfall and air temperature affect soil conditions. There are, however, certain soil factors, such as physical texture and chemical nature, which are practically independent of weather, so that it is often necessary to enquire which particular component of the whole environment is chiefly responsible for the adverse influence on the plant. Recent investigations have stressed the enormous importance of environmental influences upon the incidence of plant diseases.

It has already been stated that nitrogen in excess tends to render wheat more liable to attacks of rust. On the other hand, salts of potassium in slight excess increase resistance to rust fungi.

On heavy soils, retentive of water, varieties of apples usually free from Canker often become seriously attacked by this disease.

In connection with the soil it is now recognised that with those fruit trees like the apple and plum which are budded or grafted on stocks of a different kind, the nature of the root system of the stock exercises a profound influence on the growth of the upper part of the tree. In some cases the nature of the stock affects markedly the susceptibility of the variety to certain diseases. The variety of apple "Bramley's Seedling" is usually extremely resistant to Canker, but a short time ago I saw a number of trees of this variety, worked on an unusual stock, which were so badly cankered that some of them died. Here again we do not know in what way the stock exercised the adverse influence, though this was probably bound up with the nature of the root system.

Whereas on poor soils the larch tree is extremely liable to Canker, on soils of good quality, where the situation is otherwise suitable, Canker is almost non-existent. This is because the tree, when growing vigorously, produces cork barriers so rapidly and effectively that any considerable progress of the fungus in the bark is prevented.

Temperature is the weather factor which probably exercises the greatest influence in modifying disease-resistance in plants. Each living organism thrives best within a certain range of temperature; a little above or below this range it may continue to live with diminished vitality. Lack of vigour at unfavourable temperatures may render a normally resistant plant quite susceptible to disease. A certain parasitic fungus may have quite a different temperature for optimum growth than its host; if therefore the temperature be particularly suitable to the fungus and detrimental to the host, disease of a serious kind will probably ensue. Under reverse conditions, i.e. favourable to the host and detrimental to the fungus, there will be little or no disease.

One of the most striking investigations upon the influence of temperature on disease-resistance is that carried out recently in the United States upon the seedling blight of wheat and maize, caused by *Gibberella Saubinetii* (4). As is well known, wheat grows best at relatively low soil temperatures, whereas maize thrives best at high temperatures. The fungus which causes seedling blight of these plants grows well over a wide range of temperature. On soil infected by this fungus wheat remains unaffected if the seed germinates at a temperature of about 8° C. If, however, the wheat begins to develop at a high soil temperature (20°–28° C.), there is great mor-

tality from the disease. On the other hand, maize at a high temperature (24°–28° C.) is hardly affected at all, but it is seriously attacked at a low temperature (8°–16° C.). Further enquiry has shown that where wheat and maize are growing at unfavourable temperatures the nature of the outer cell walls is different from the normal, and the walls are thinner. This change in the character of the cell walls renders the plants much more susceptible to penetration by the hyphae of the fungus, and so the plants become seriously diseased. With respect to this disease, it has also been shown that both wheat and maize are affected severely at all temperatures when grown in soils of very low water-content. Here again an adverse condition for the growth of the crop plant renders it extremely susceptible.

Temperature is sometimes so unfavourable to a parasitic fungus that the latter has no chance of attacking its host. In this way the cultivated plant escapes disease, not because of any inherent property, but because the temperature is so adverse to the fungus that it cannot even initiate infection. A striking example of such an effect of temperature is seen in the distribution of the disease known as Onion Smut in the United States. This disease, which can only be established in the seedling stage, cripples the growth of the very young plants and produces unsightly black streaks of smut spores towards the base of the plant. Onion Smut is prevalent in the northern part of the United States, but is unknown in the south. Investigation has shown that the absence of the disease in the south is due to such high soil temperatures that most of the fungus spores do not germinate and are therefore incapable of causing infection (13). A temperature of 29° C. either inhibits germination of the spores or kills the delicate germ tubes if the spores do germinate.

A somewhat similar phenomenon is met with in the distribution of *Puccinia graminis* (Black Rust of cereals) in the southern United States. In this region the fungus occurs commonly on wheat, but it never affects the barberry, as it does in the north. The reason for this is that the black teleutospores formed on the wheat straw lose their vitality during the warm winters of the south and so cannot infect the barberry in the spring. In the north the cold winter preserves the life of the teleutospores and so the barberry can be infected. The same considerations probably account for the fact that barberry bushes are not infected in Australia although Black Rust is all too common there on wheat.

With the marked influence which environment exercises upon

the expression of disease-resistance it is not surprising that a variety which is practically immune to attack during one period of the year may be very susceptible at another. The variety of wheat "Little Joss" is usually very resistant to Yellow Rust, but I have seen fields of it in February and March which were yellow with this rust. When such wheat began to grow actively again in April and May the new foliage was entirely free from rust.

Some particular part of the shoot system of a plant may alone be susceptible to disease, whereas the whole of the shoots of closely related varieties may be susceptible. A variety of wheat "Norka" was recently sent to me from the United States as being very highly resistant to mildew there. One of the most critical tests for mildew-resistance is to grow the plant in a greenhouse, for if the resistance is not extremely marked mildew develops abundantly on the foliage. This variety "Norka" grown in a greenhouse remained quite free from mildew until the ears were fully developed, when the fungus developed slightly on the glumes.

In recent investigations on virus diseases of plants there has been encountered a phenomenon which in some respects is very similar to a well-known phenomenon in human pathology. With certain diseases like typhoid and cerebro-spinal meningitis some individuals can be infected with the bacteria of these diseases without becoming ill. Persons who are tolerant of these bacteria are said to be "carriers" of disease. They may, of course, be sources of infection in a healthy community.

With certain virus diseases of potatoes some varieties which appear to be perfectly healthy may be shown by suitable experiments to be "carriers" of specific viruses. By grafting one of these "carriers" on to a healthy but susceptible plant the virus is transmitted from the "carrier" into the susceptible plant, in which the characteristic symptoms of the virus disease quickly appear. At present we know very little as to the nature of virus diseases in plants, but in the varieties which are "carriers" presumably the virus is tolerated by the host or is present in it in a latent condition. In some other virus diseases of plants "carriers" have been shown to exhibit symptoms of the presence of the virus by changing the environmental conditions.

From the stress which has been laid upon the modification of disease-resistance by environmental conditions it may be concluded that the genetic quality of resistance is of little importance. That is certainly not true. The resistant quality of the variety is still

present even though it may be partly masked by the influence of an adverse environment.

Soon after the re-discovery of Mendel's Law of Heredity, Biffen (2) showed that susceptibility and resistance to Yellow Rust in wheat were definite hereditary entities transmitted in accordance with that law. On crossing a susceptible wheat with a resistant one the hybrids all proved to be susceptible; on self-pollinating these hybrids, the plants of the next generation segregated in the proportion of three susceptible to one resistant. In this example a single hereditary factor was responsible for susceptibility or resistance. Since this discovery much work has been done on the elucidation of the transmission of susceptibility or resistance to disease in plants. With regard to Yellow Rust of wheat susceptibility is dominant to resistance, but with Wheat Mildew resistance is dominant to susceptibility. The transmission of susceptibility or resistance is also sometimes more complicated than in the example outlined, and is dependent upon more than one factor. This is the case in the inheritance of susceptibility to potato Wart Disease.

With the clue afforded by the re-discovery of Mendel's law plant-breeders, the whole world over, are attempting to introduce new varieties of cultivated plants which will be more resistant to disease than those formerly grown. Many varieties of plants which are highly resistant to disease are of little commercial value because of low cropping capacity or of some other defect. Plant-breeders now often have it within their power to combine the character of disease-resistance of one variety with the heavy-cropping capacity or other desirable quality of a susceptible variety. Considerable progress has already been achieved along these lines.

It may be argued that the future control of plant diseases lies in the hands of the plant breeder. This is only partly true. Unexpected difficulties are sometimes encountered in breeding work, in which it appears impossible to combine the character of disease-resistance with the fine quality and heavy yield of susceptible varieties. Besides, all Nature being in a state of flux when any long period of time is taken into consideration, it must be remembered that pathogenic organisms themselves may change, and, with increasing virulence, may attack varieties of crop plants hitherto resistant. It is particularly the province of the plant pathologist to ascertain the conditions of growth of cultivated plants which are least favourable to attack by parasites, and to prevent disease by applying the methods of plant sanitation. The best results in the control of plant

diseases are likely to be achieved by the mutual co-operation of plant breeder and plant pathologist. With plants as with human beings we cannot foresee the time when there will be no more disease and no more death.

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